Predicting differential effects of climate change at the population level with life-cycle models of spring Chinook salmon

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Abstract

Habitat conditions mediate the effects of climate, so neighboring populations with differing habitat conditions may differ in their responses to climate change. We have previously observed that juvenile survival in Snake River spring/summer Chinook salmon is strongly correlated with summer temperature in some populations and with fall streamflow in others. Here, we explore potential differential responses of the viability of four of these populations to changes in streamflow and temperature that might result from climate change. First, we linked predicted changes in air temperature and precipitation from several General Circulation Models to a local hydrological model to project streamflow and air temperature under two climate-change scenarios. Then, we developed a stochastic, density-dependent life-cycle model with independent environmental effects in juvenile and ocean stages, and parameterized the model for each population. We found that mean abundance decreased 20–50% and the probability of quasi-extinction increased dramatically (from 0.1–0.4 to 0.3–0.9) for all populations in both scenarios. Differences between populations were greater in the more moderate climate scenario than in the more extreme, hot/dry scenario. Model results were relatively robust to realistic uncertainty in freshwater survival parameters in all scenarios. Our results demonstrate that detailed population models can usefully incorporate climate-change predictions, and that global warming poses a direct threat to freshwater stages in these fish, increasing their risk of extinction. Because differences in habitat may contribute to the individualistic population responses we observed, we infer that maintaining habitat diversity will help buffer some species from the impacts of climate change.

Keywords: conservation, endangered species, habitat diversity, life-history model, population dynamics, population viability model, stream flow

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Introduction

Both ecological and climatic processes are characterized by hierarchies of spatial heterogeneity, making the interplay between population dynamics and climate change extremely complex (Pearson & Dawson, 2003). When predicting the effects of climate change, most authors cope with this complexity by reducing ecological heterogeneity to the presence/absence of particular species or community types (e.g. Thuiller, 2004).

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Despite widespread recognition that this approach oversimplifies the ecology, few studies have explored potential consequences of within-species variation. Populations within a species may respond differently to climate change because a variety of factors, such as species interactions, physiology, genetic architecture, behavior, and habitat mediate environmental effects on individuals (Murphy & Weiss, 1992; Etterson & Shaw, 2001; Hilborn *et al.*, 2003). We currently have limited ability to assess how different the responses are likely to be.

Just as climate change may differentially affect conspecific populations, it may also differentially affect life

stages within individuals. This ontogeny/climate interaction occurs because individuals' physical tolerances and habitat usage may change through ontogeny and because they may migrate among habitat types. Species that undergo long-distance migrations are especially prone to this effect because their migrations take them to geographic regions with distinct climates. They exemplify the delicate balance of ecological processes across space and the interconnectedness of radically different ecosystems.

Pacific salmon (*Oncorhynchus* spp.) are renowned for fine-tuned local adaptation (Taylor, 1991), often combined with long-distance migrations between life stages. Salmon spawn in freshwater, but complete most of their growth in nutrient-rich ocean waters. Variable ocean conditions have strong effects on marine survival, and are typically considered the dominant driver of salmon abundance (Beamish & Bouillon, 1993; Mantua *et al.*, 1997; Francis & Mantua, 2003; Levin, 2003; Tolimieri & Levin, 2004). However, the tight link between life-history strategies and freshwater conditions suggests that freshwater climates can impose strong selection on these populations by affecting juvenile survival (Brannon *et al.*, 2004; Waples *et al.*, 2004). Our previous analysis (Crozier & Zabel, 2006) of over 130 000 juvenile survival histories over 14 years in 15 populations revealed that populations appear to differ in their responses to annual variation in the weather. These differences appeared despite the fact that these populations have similar life-history characteristics

and share a relatively small geographic area, in the 36 260 km^2 Salmon River basin, in central Idaho, USA (Fig. 1). In populations that inhabit wider and warmer streams, summer temperature is strongly negatively correlated with juvenile survival. In populations that inhabit narrower and cooler streams, fall stream flow is strongly positively correlated with juvenile survival.

Climate models predict that in snow melt-dominant rivers of the Pacific Northwest, global warming will cause summer stream temperatures to increase, and summer–fall flow levels to decline (Hamlet & Lettenmaier, 1999; Mote *et al.*, 2003). Temperatures that are above optimal impede developmental processes (e.g. smoltification) and predator-avoidance behavior (Marine & Cech, 2004), and reduce growth rates (Bisson & Davis, 1976). Extremely low flows may decrease survival in small streams by reducing potential habitat, which increases competition for food and vulnerability to predators. Consequently, we predict that global warming will lower juvenile survival in all of these populations. However, the expected rates of change in temperature and flow differ within and between climate-change scenarios. Here, we explore the potential for such relatively subtle differences between populations to affect their responses to long-term directional change in the environment due to global warming. More specifically, we use a stochastic, density-dependent life-cycle model to predict population viability under several climate scenarios. To capture the variability among populations, we developed population-
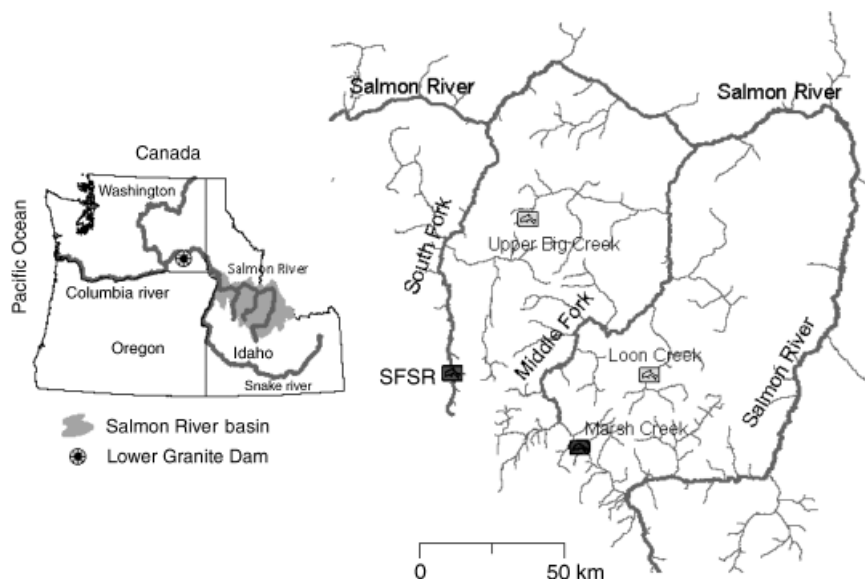
Fig. 1 These maps of the study area show the location of the Salmon River basin in the Pacific Northwest of the United States (left), and the locations of the four populations described in the text (fish symbols, right). Survival is estimated from the natal stream to Lower Granite Dam. The two temperature-sensitive populations have lighter shading (Upper Big Creek and Loon Creek), and the two flow-sensitive populations have darker shading (SFSR and Marsh Creek). SFSR, South Fork Salmon River.

specific models for four populations with each model characterized by unique responses to freshwater conditions. We retain the historical pattern of variation in ocean conditions and ocean growth and survival rates because future ocean conditions are very uncertain. Finally, we conduct a sensitivity analysis that incorporates empirical estimates of uncertainty in each parameter and retains the observed correlation structure between parameters to determine how sensitive our results are to realistic uncertainty in model inputs.

Methods

Life-cycle model

To predict potential effects of climate change on these populations we used a stochastic, density-dependent life-cycle model, modified from Zabel *et al.* (2006). We based our model on the complex life history of Snake River spring/summer Chinook salmon that spawn in the Salmon River basin of Idaho, 1100–1500 km from the Pacific Ocean. All populations are 'stream-type,' which means that juveniles spend a whole year in freshwater streams before migrating to the ocean. These salmon then spend 1–4 years in the ocean before returning to natal streams to reproduce. We modeled this life cycle in five annual life stages that may include multiple life-history stages. The annual time steps are referenced to the time adults begin upstream migration. The first stage includes upstream migration of adults, spawning, and egg to 1-year-old (parr) survival; the second stage includes the survival over the following year, during which freshwater environmental conditions affect parr to 2-year-old (smolt) survival, and downstream migration. The third stage includes estuarine residence and the first year in the ocean; the fourth and fifth stages include the later ocean age classes.

We project the age structure of each of the four populations through time as the vector $\mathbf{n}(t)$, using a stochastic transition matrix $\mathbf{A}(t)$ as described by Caswell (2001):

$$\mathbf{n}(t+1) = \mathbf{A}(t) \cdot \mathbf{n}(t). \tag{1}$$

Our matrix includes survival probabilities, s, a fertility function F, and the propensity to breed at a given age i, b_i:

$$\mathbf{A}(t) = \begin{bmatrix} 0 & 0 & 0 & b_4 \cdot s_u \cdot F_p(\mathbf{n}(t)) & s_u \cdot F_p(\mathbf{n}(t)) \\ s_{2,p}(t) \cdot s_d & 0 & 0 & 0 & 0 \\ 0 & s_3(t) & 0 & 0 & 0 \\ 0 & 0 & (1-b_3) \cdot s_o & 0 & 0 \\ 0 & 0 & 0 & (1-b_4) \cdot s_o & 0 \end{bmatrix}. \tag{2}$$

The first row determines the number of 1-year-olds produced per adult returning to the mouth of the Columbia River. The returning adults are converted to spawners based on upstream migration survival (s_u), which includes harvest (H). The fertility function (F), which converts spawners to 1-year-olds, varies with the age and density of spawners. The shape of the fertility function varies across populations, denoted p. Adults return to freshwater in their third, fourth, or fifth year. However, virtually all of the 3-year-old fish that return to freshwater are 'sneaker' males that compete with older males and do not change overall fertility. In addition, 5-year-old females are more fecund than 4-year-olds, and this is reflected in the fertility function, which is described in detail below. Survival through the second year is based on survival through the freshwater rearing stage (s_2), and downstream migration (s_d). Survival in the freshwater rearing stage is specific to a population and varies across time in response to environmental conditions. Third-year survival (s_3), varies in response to ocean conditions specified yearly. Survival through the fourth and fifth years is determined by ocean survival (s_o). The age of maturity varies within populations, and this is captured by specifying age-specific propensity to breed (b_i), which determines the proportion of fish of age i that return to spawn.

Downstream and upstream migration survival, s_d and s_u, are held constant over time, reflecting current river and harvest management. Nearly 80% of smolts are currently transported in barges downriver in an attempt to reduce mortality caused by the eight major hydroelectric dams along the migration route. We estimated downstream survival using the equation

$$s_d = p_t s_t D + s_r (1 - p_t), \tag{3}$$

where p_t is the proportion of fish that are transported in barges, s_t is their survival during transport, and s_r is the riverine survival of fish that migrate on their own. Transported fish typically have lower adult return rates than fish that migrated through the river independently, and D describes this ratio (Williams *et al.*, 2005). We incorporate D in the second time step for mathematical simplicity. We estimated upstream survival using the equation

$$s_u = s_h s_a (1 - H), \tag{4}$$

where s_h is survival through the hydropower system, s_a is adult prespawning survival above the dams, and H is the proportion of migrants that are harvested. Parameter estimates are provided in Table 1.

Table 1 Parameter estimates that are shared by all populations

Parameter	Point estimate (SE)	Description	Equations	Reference
Downstream survival				
p_t	0.8	Proportion transported	(3)	*,†
D	0.533	Latent mortality	(3)	*,†
s_t	0.98	Barge survival	(3)	*,†
s_r	0.486	Survival of nontransported fish	(3)	*
Ocean survival				
β_{PDO}	−2.54 (0.09)		(6)	†,‡
β_{Apr}	0.69 (0.2)		(6)	†,‡
β_{May}	−1.66 (0.09)	Regression coefficients for third year survival	(6)	†,‡
β_{Jun}	0.49 (0.15)		(6)	†,‡
σ_3^2	0.26 (0.08)		(6)	†,‡
s_o	0.8	Later ocean survival	(2)	‡
Upstream survival				
s_h	0.806	Survival through hydropower system	(4)	*,†
H	0.07	Harvest in river	(4)	*
s_a	0.9	Adult prespawn survival in tributaries	(4)	§
Fertility				
b_3	0.0345	Propensity of 3-year-old fish to breed	(2)	‡
b_4	0.4592	Propensity of 4-year-old fish to breed	(2)	‡
f_5	1.26	Fecundity advantage of 5-year-olds	(8)	‡

The parameters in parentheses are derived from others in the table.
*Williams *et al*. (2005).
†Updated with unpublished data.
‡Zabel *et al*. (2006).
§Kareiva *et al*. (2000).

Estimating juvenile freshwater survival (s_2)

In the model, the key difference between populations in their response to climate occurs in the freshwater stages; ocean climate, on the other hand, affects the survival of all populations similarly. We modeled juvenile rearing survival (s_2) as a linear function of either temperature or flow, depending on the population, based on a previous study described in Crozier & Zabel (2006). To make our survival estimates as comparable as possible between populations and between historical and climate-change scenarios, we used the gridded historical air temperatures from 1915 to 2002 that are input to the hydrology model rather than those from a particular weather station. These air temperatures are based on weather station data from the US National Climatic Data Center, but they are projected onto a grid with a resolution of 0.125° latitude and longitude (see Lettenmaier, 2000 for methodological details). We simulated monthly mean stream flow for the Salmon River at Salmon, Idaho with the variable infiltration capacity (VIC) macroscale hydrologic model (Liang *et al*., 1994) implemented at 0.125° latitude and longitude resolution (Hamlet *et al*., 2005).

Crozier & Zabel (2006) identified four population clusters that differed in their annual variability in survival. Summer average air and stream temperatures were the best predictors of survival for two population clusters, including two of the populations used here, Loon Creek and Upper Big Creek; fall stream flow was the best predictor of survival in the other two population clusters, including Marsh Creek and South Fork Salmon River (SFSR, Fig. 1). For simplicity, we will refer to each population as either temperature or flow sensitive. Following their approach, we used the yearly varying cluster survival estimates and applied the population-specific offset to estimate annual population-specific survival for this study. Because air temperatures have a much better historical record than and are strongly correlated with stream temperatures in this basin (Donato, 2002), we used air temperatures to predict survival in this analysis.

For each of the four populations, we regressed logit-transformed survival from 1992 to 2005 against June air temperature or October flow $x_p(t)$, as appropriate for the population p,

$$\text{logit}(s_{2,p}(t)) = \beta_{0,p} + \beta_{1,p} x_p(t) + \varepsilon_{t,p}, \tag{5}$$

where ε_p is normally distributed, to produce the parameter estimates shown in Table 2. Air temperature estimated for our study region, at latitude 45.1875°N

Table 2 Parameter estimates and standard error used in Eqns (5) and (8), and the sensitivity analysis

Parameter	Temperature-sensitive		Flow-sensitive	
	Loon	Upper big	Marsh	SFSR
β_0	0.89 (0.73)	−0.15 (0.75)	−3.65 (0.58)	−3.94 (0.58)
β_1	−0.25 (0.08)	−0.202 (0.08)	0.092 (0.027)	0.083 (0.027)
a	2762 (167.6)	5829 (295.4)	981 (109.7)	2908 (671.1)
b	0.06513 (0.0042)	0.06727 (0.00373)	0.00607 (0.00159)	0.00468 (0.00161)
φ	4	0.7	0.1	0
σ^2	0.00058 (0.00003)	0.15017 (0.0062)	0.43689 (0.0237)	0.62276 (0.0234)

and longitude −114.8125°W, from 1992 to 2005 was negatively correlated with survival in Loon Creek ($r^2 = 0.58$, $P = 0.017$), and Upper Big Creek ($r^2 = 0.48$, $P = 0.04$). Simulated mean October stream flow was positively correlated with survival in the other two populations, Marsh Creek ($r^2 = 0.54$, $P = 0.006$) and SFSR ($r^2 = 0.45$, $P = 0.009$). We used the regression Eqn (5) to estimate survival in earlier years as a function of historical temperature or flow in the stochastic population viability analysis described below. We used a logit-transformation in all survival analyses because survival is constrained between 0 and 1.

In considering the validity of our extrapolation to warmer conditions, it is important to realize that the streams we focus on here are relatively cool (maximum weekly mean temperatures are about 12–13 °C). Other Chinook salmon-bearing streams in this basin are ∼3–4 °C warmer. Therefore, adding 3 °C to cool streams does not expose fish to lethal conditions, nor is it beyond conditions we have observed during the study, albeit among different populations. The effect of temperature in these streams is presumably indirect, (i.e. mediated by food supply or predation effects).

Ocean survival (s_3 and s_o)

We followed the approach of Zabel *et al.* (2006) to relate third-year survival (s_3) to monthly indices of the Pacific Decadal Oscillation (PDO)

$$\text{logit}(s_3(t)) = \beta_{\text{PDO}} + \beta_{\text{Apr}}PDO_{\text{Apr}}(t) + \beta_{\text{May}}PDO_{\text{May}}(t) + \beta_{\text{Jun}}PDO_{\text{Jun}}(t) + \varepsilon_t. \tag{6}$$

This relationship was based on data representing all Snake River spring/summer Chinook salmon. Here, we assume that all populations share the same relationship because they have similar temporal and spatial migration patterns. PDO index values came from Mantua (2005). The error term ε is distributed as $N(0,\sigma_3^2)$. We accounted for the covariance in the consecutive

monthly PDO indices by applying equation 20.34 from Zar (1984) to produce the stochastic term. Following Zabel *et al.* (2006), we applied a constant survival rate of 0.8 for the remaining years in the ocean (s_0), which preserves the overall amount of error in the smolt-to-adult survival data from which the third-year survival estimates were derived.

Density-dependent juvenile recruitment

The streams vary greatly in size and condition, so fertility and the impacts of density are likely to differ between populations. To describe these differences, we used spawner count estimates from each population from 1962 to 2002 (Biological Review Team, 2003) to fit stream-specific recruitment functions. When the spawner counts consisted of redd (salmon nest) counts, we assumed a spawner-to-redd ratio of 1.82 (Beamesderfer *et al.*, 1997). We applied the Beamesderfer *et al.* (1997) method of calculating recruits from a given spawner year. Specifically, we used the age of returning adults to assign them to a brood year, so that recruits from a given brood year are counted regardless of when they returned to spawn. We then back-calculated the number of parr (1-year-olds) separately for each population as follows:

$$n_{1,p}(t) = \frac{y_4(t+3) + y_5(t+4)}{s_{2,p}(t) \times SAR(t+1) \times s_a}, \tag{7}$$

where $y_4(t+3)$ is the number of 4-year-old spawners, $y_5(t+4)$ is the number of 5-year-old spawners, $s_{2,p}(t)$ is survival from parr to smolt, $SAR(t+1)$ is the smolt-to-adult return rate measured at the uppermost dam (Petrosky *et al.*, 2001; Williams *et al.*, 2005), and s_a is the prespawn mortality that occurs above the dams. We then fit a Beverton–Holt function for each population p to predict the number of parr per spawner as a function

of the number of spawners y as

$$F(y_p(t)) = \frac{n_{1,p}(t+1)}{y_p(t)} = \frac{a_p}{1 + b_p y_p(t)} + \varepsilon_t. \qquad (8)$$

In Eqn (8), 5-year-old spawners are multiplied by a fecundity factor, f_5, to reflect their greater fecundity compared with 4-year-olds ($y = y_4 + f_5 \cdot y_5$). The error around this estimate, ε, is normally distributed after a Box–Cox transformation, which accounts for heterogeneity in variance (Box & Cox, 1964). We selected the Box–Cox parameters σ^2 and φ such that the error is distributed independently as $N(0, \sigma^2 \cdot F(y \,|\, a, b)^\varphi)$, where F is the Beverton–Holt function above. As suggested in Seber & Wild (1989), we estimated the four parameters, a, b, σ^2, and φ simultaneously (Table 2).

Population viability analysis

To predict the effects of climate change, we wanted to simulate population trajectories under various environmental conditions. We used the life-cycle model just described to project population abundance into the future. This model incorporated environmental conditions in both parr-to-smolt survival (s_2) and early-ocean survival (s_3). Differences between populations arose from (1) different initial population sizes, (2) population-specific spawner-recruit parameters [Eqn (8)], and, (3) population-specific parr-to-smolt survival parameters [Eqn (5)]. Stochasticity in the spawner-recruit function [Eqn (8)] and the ocean survival function [Eqn (6)] drove variation among simulations within a population. We started each run with the number of spawners observed in 2001, the most recent census available: Loon Creek, 520; Marsh Creek, 359; Big Creek, 286, and SFSR, 1203. We back-calculated the number of fish in the nonspawning age classes by using the mean s_2 and s_3 over the historical record. We then ran the simulations using the environmental conditions appropriate for each test 100 000 times for each population.

We considered diverse viability metrics because each captures a different aspect of population performance and might respond differently to environmental change. Because Chinook salmon stay in the ocean until they are ready to spawn, a population may not be extinct even if it has no spawners in a given year. Therefore, most of our viability metrics are based on the running mean number of spawners over 4 years. First, we characterized population viability in terms of the minimum and mean abundance (i.e. minimum or mean of the running mean) of spawners per population over the full length of the meteorological record (1915–2002, 88 years) in each simulation. Second, we determined the probability that each population would drop below a quasi-extinction threshold. The threshold was population-specific because population size estimates are based on index reaches of different size. The threshold was based on the estimated carrying capacity for each population, using the Beverton–Holt equation to define parr carrying capacity (a/b). We applied the mean historical parr-to-smolt survival (s_2) and smolt-to-adult return to 10% of parr-carrying capacity to calculate the threshold number of spawners. These running mean thresholds were: Loon Creek, 22; Marsh Creek, 73; Big Creek, 23, and SFSR, 186. Although the exact threshold is somewhat arbitrary, these numbers were very similar to the minimum 4-year running mean abundance observed in the historical record of spawner counts, which began in 1962. The populations in this study are already at dangerously low levels, so dropping below these levels is cause for increased concern. Finally, we assessed average population annual growth rate λ over the 88 years of each simulation by calculating the geometric mean of $\lambda(t)$, where $\lambda(t) = N(t+1)/N(t)$. Unlike the other viability metrics, λ was based on annual spawner counts, not on the running mean.

Climate scenarios

To determine whether the different forcing factors between the populations are likely to produce different responses to climate change, we identified two climate-change scenarios that spanned a range of reasonable predictions for this region. We created a relatively moderate, 'composite' scenario by taking the average monthly changes in temperature and precipitation across 10 General Circulation Models prepared for the Intergovernmental Panel on Climate Change Fourth Assessment (IPCC; Hadcm3, Echam5, CCSM3, PCM1, CNRM_CM3, CSIRO_MK3, Miroc_3.2, IPSL_CM4, CGCM_3.1, and GISS_ER – see Mote *et al.*, 2005). For the 2040 time frame, this produced a moderately warm scenario (annual average temperature rose about 1.77 °C), in which wetter winters balanced drier summers, with little change in annual average precipitation compared with the historic level. To capture a more severe scenario, we used the hottest and driest of those general circulation model (GCM) products – the CCSM3 model output. Annual averages for this scenario are about 2.6 °C warmer and 6.9% drier than the historic climate. The GCM simulations assume a $1\% \, \text{yr}^{-1}$ increase in equivalent CO_2 or the A2 emissions scenario used by the IPCC (2007).

To predict local changes in temperature and precipitation from the GCM output, we applied the 'delta' method of downscaling following the approach outlined by Hamlet & Lettenmaier (1999). In this approach, we use monthly changes in temperature and precipitation derived from the climate-change scenarios to

perturb an observed daily time-step climate record from 1915 to 2002 (Hamlet *et al.*, 2005), which then drives the VIC hydrologic model. The adjustment factor, or delta, was the GCM prediction for each calendar month after 50 years of warming. For example, if the historical mean temperature in June 1960 was 9 °C, and the delta value for June was 2.3 °C, then the predicted temperature in the 2040s climate would be 11.3 °C. In this approach, we examine to first order the hydrologic effects of projected changes in mean climate, but intentionally ignore the potential impacts of more complex changes in the climate system by largely preserving the observed climate variability (Hamlet & Lettenmaier, 1999; Snover *et al.*, 2003). Decadal climate variability associated with the PDO, for example, is essentially identical to that observed in the 20th century in the experiments carried out here. We chose this approach because the impacts of global warming on decadal-scale climate variability remain very uncertain, and because our primary goal was to focus on the ecological effects of plausible changes in freshwater conditions.

Sensitivity analysis

To characterize the relative importance of parameter estimates on model outcome, we conducted a sensitivity analysis. We followed the technique described in Zabel *et al.* (2006), and which was originally proposed by McCarthy *et al.* (1995). To capture potential interactions between parameters and explore a large region of parameter space, we produced 2000 parameter sets by randomly varying population-specific and climate-related parameters simultaneously (a, b, σ^2, β_0, β_{PDO}, β_{Apr}, β_{May}, β_{Jun}, σ_3^2). In order to have the variance in the fertility function increase linearly, we left φ at the point estimate. For each set, we drew each parameter from a uniform distribution spanning the range of its 95% confidence interval to incorporate our best estimate of uncertainty in parameter values. We retained the correlation structure within the regression parameters for freshwater and marine survival. For freshwater survival, we drew randomly from a normal distribution within the confidence interval around each estimate of survival for a given year for each population to generate 2000 datasets, and for each dataset we fit the regression in Eqn (5). For marine survival, we randomly drew β_{PDO} and β_{Apr} from their confidence intervals because they were not correlated with each other, but assigned β_{May} and β_{Jun} based on the variance/covariance matrix of the regression parameters.

We then ran the population viability model with 10 simulations per set of parameter values, tracking mean population abundance and whether the population fell below the minimum observed threshold value. This procedure produced 20 000 simulations (2000 parameter sets $\times$ 10 replicates set^{-1}). We then conducted a multiple linear regression of simulation outcome as a function of all of the parameter values. Thus, we modeled mean abundance, for example, as a function of 10 parameter values. Because the criterion of whether the population fell below the threshold produced a binary outcome of either 0 or 1, we used a generalized linear model with a binomial link function (logistic regression) to model this outcome. We standardized the coefficients of each of these regressions by dividing by their standard error to put them all on the same nondimensional scale. To compare the weights of parameters across models, we further standardized them by dividing all coefficients within a model by the coefficient with the greatest weight. Therefore, within a model, the most important coefficient is always ± 1.

Results

Physical changes

Both the composite and CCSM climate-change scenarios produced lower fall flows and higher summer temperatures, with the CCSM scenario having the greater effect on both variables (Fig. 2). Despite the slight increase in precipitation in the composite scenario, median October flow declined from the baseline (i.e. historic climate) scenario of 23.0 to 20.2 m^{3}s^{-1} in the composite scenario, and to 17.9 m^{3}s^{-1} in the CCSM scenario. This shift in the median produced 4.5% and 9.1%, respectively, of simulated flows that were below the historical minimum. June temperature rose 2.1 °C in the composite scenario, and 3.1 °C in the CCSM scenario. Consequently, 13.6% and 30.7%, respectively, of the simulated temperatures were above the historical maximum.

Effects on population dynamics and viability

Lower October flow caused parr-to-smolt survival to decline 18–19% in the composite scenario, and 34–35% in the CCSM scenario for SFSR and Marsh Creek populations (Fig. 3). The rise in temperature caused survival in Loon and Big Creeks to decline 34% and 31%, respectively, in the composite scenario, and 47% and 43% in the CCSM scenario (Appendix A).

Mean population size declined in both climate scenarios for all populations (Fig. 4). In the composite scenario, population sizes declined 20–37%, and in the CCSM scenario they declined 37–50% (Appendix A). A pattern similar to that seen with parr-to-smolt survival occurred with abundance: the composite scenario had a greater effect on the temperature-sensitive populations, especially Big Creek, than the flow-sensitive popula-
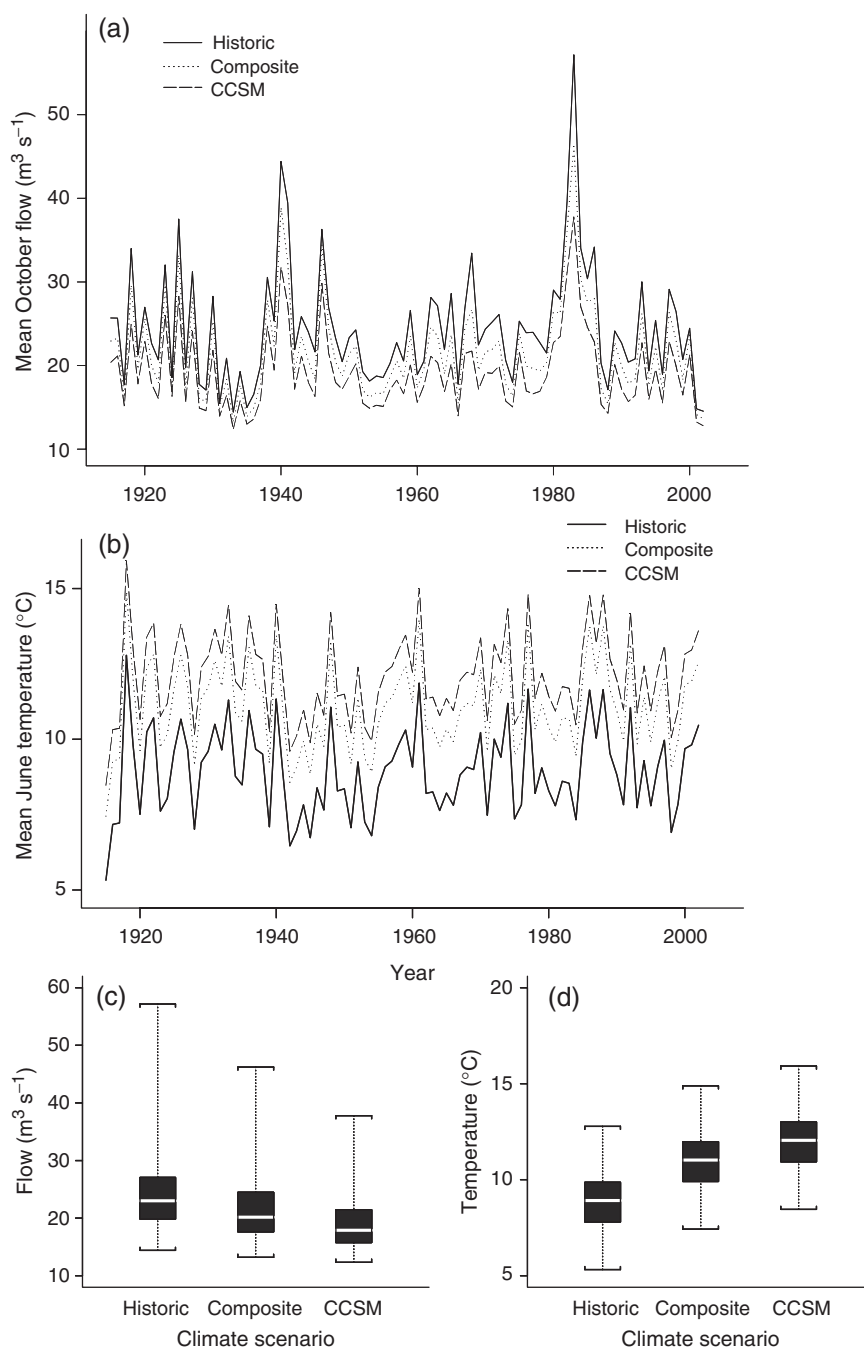
Fig. 2 (a) Streamflow and (b) temperature input for the three climate scenarios described in the text. Summaries of this same data are shown in (c) for streamflow and (d) average June temperature: the line shows the median, the boxes enclose the first to third quartile range, and the whiskers show the most extreme values.
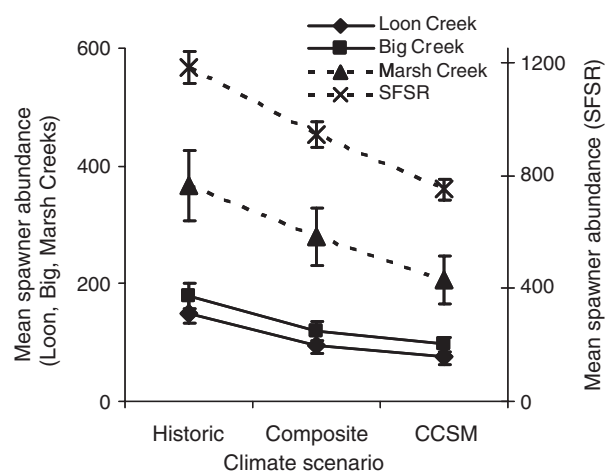
tions. Minimum abundance (median across all simulations) followed the same pattern as mean population size (Appendix A). Loon, Big, and Marsh Creeks had minimum running mean abundances from four to 13 fish in half of the CCSM simulations, which was about half of the median minimum in the current climate (50–64% lower).

The probability that abundance would sink below critical thresholds increased markedly in both climate-change scenarios, and the climate scenario affected the relative risk of populations in the probability of quasi-extinction (Fig. 5). This occurred despite the fact that density-dependent processes compensated for declines in parr-to-smolt survival to some extent. Fertility, (i.e.
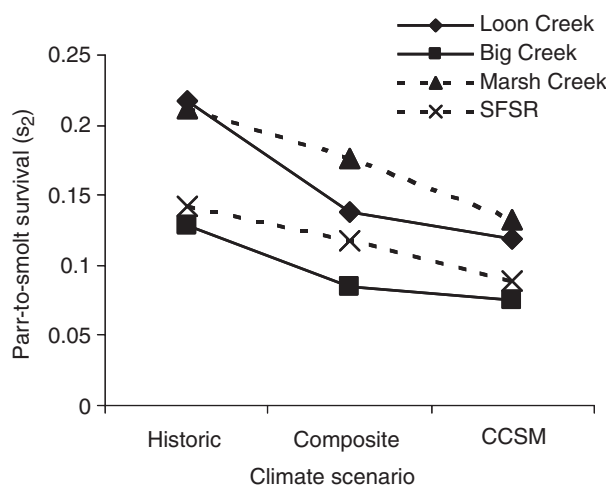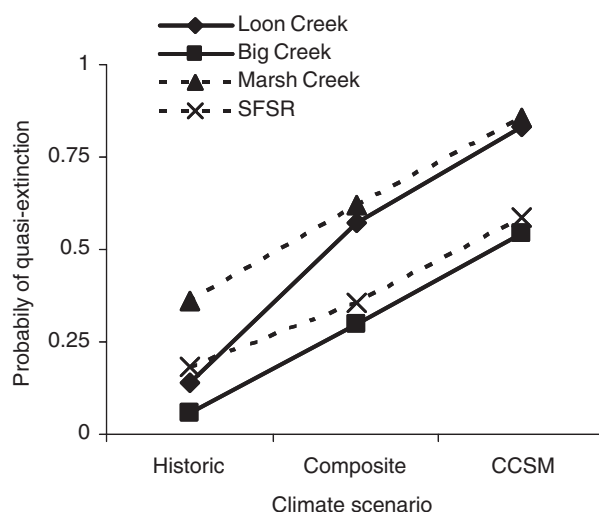
Fig. 3 Mean parr-to-smolt survival over the time series for each climate scenario. Solid lines represent temperature-sensitive populations, and dotted lines represent flow-sensitive populations.
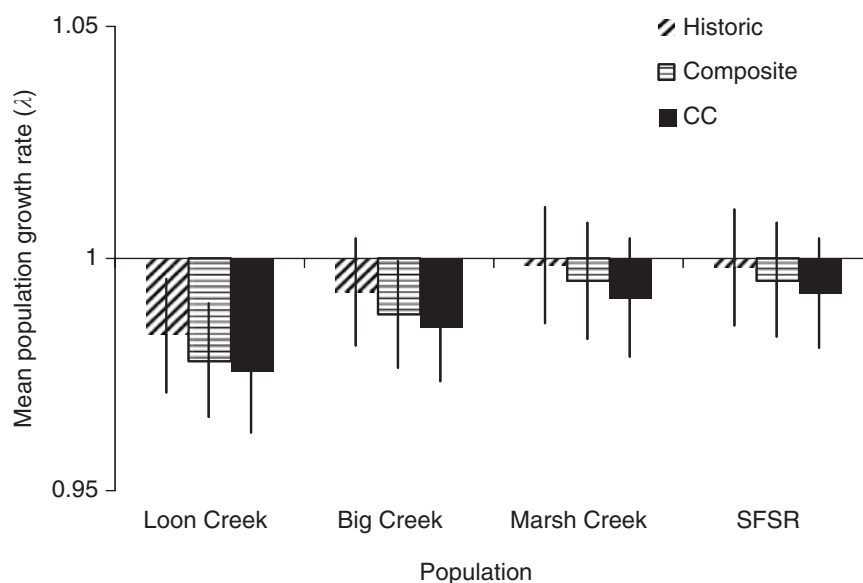

Fig. 5 Quasi-extinction probabilities under different climate scenarios. Solid lines represent temperature-sensitive populations, and dotted lines represent flow-sensitive populations.

the mean number of parr per spawner), increased in all populations by 15–60% in the composite scenario, and by 34–100% in the CCSM scenario. Still, the risk of dropping below the record historical low abundance shifted from a range of 6–36% in the current climate to 30–62% in the composite scenario, and to 54–86% in the CCSM scenario. Population growth rate declined under both climate-change scenarios, although the differences in mean were small compared with the standard error across simulations (Fig. 6).

Fig. 4 Mean spawner abundance ($\pm$SD) for each scenario. SFSR is much larger than the other populations, and is therefore drawn with a secondary *y*-axis. Solid lines represent temperature-sensitive populations, and dotted lines represent flow-sensitive populations. SFSR, South Fork Salmon River.

Sensitivity analysis

The sensitivity analysis showed that uncertainty in mean ocean survival (β_{PDO}) had the greatest impact on population abundance and the probability of extinction for all populations and scenarios (Fig. 7). Uncertainty in the freshwater survival parameters had relatively little impact on model outcome, which indicates that our results are robust to small changes in the functional relationship between survival and environmental factors. Climate scenarios affected the importance of freshwater survival parameters (β_0) differently for temperature-sensitive and flow-sensitive populations. The relative important of these parameters increased with the severity of climate conditions for Loon and Big Creeks, and decreased for Marsh and SFSR. This difference likely reflects the negative correlation between survival and temperature, and the positive correlation between survival and flow. Regardless, the absolute value of the weights of these parameters was less than or equal to the density dependent and ocean survival parameters in all populations.

Discussion

The degradation in population viability in response to freshwater climate change predicted by our models is alarming. We predict that mean population abundance will decrease by up to 50% (Fig. 4), and probabilities of falling below critical thresholds will increase by several-fold (Fig. 5). While uncertainty about these predictions clearly exists, we used realistic climate-change scenarios and empirically based survival relationships. Our

Fig. 6 Mean λ ($\pm$SD) for each population, under each climate scenario. Solid lines represent temperature-sensitive populations, and dotted lines represent flow-sensitive populations.

sensitivity analysis shows that our results are consistent across a reasonable range of parameter values describing the relationship between freshwater survival and environmental conditions. We also assumed compensatory dynamics in the form of the Beverton–Holt recruitment curve, but recruit dynamics could not reverse the predicted declines in abundance or the increased likelihood of quasi-extinction. Therefore, we believe the approximate magnitude of our predictions is realistic, and a reasonable probability exists that our predictions will be realized if climate changes as in the models.

A moderately encouraging aspect of our results is that populations within a species will likely respond differentially to climate change – long-term differences in population viability may result from subtle variation between populations in habitat conditions and environmental forcing factors. The populations compared here occupy very similar habitat, experience essentially the same weather, and have no obvious differences in behavior. Given the overall similarities, the different responses to 'moderate' composite climate change are striking. Unfortunately, these scenarios were much less 'moderate' for the temperature-sensitive populations, and in fact were almost as bad as the 'extreme' CCSM scenario. Nonetheless, more generally, variability in among-population response to climate can potentially serve as a buffer for the entire species (c.f. Hilborn *et al.*, 2003), and may be important for metapopulation dynamics. In a metapopulation, independent dynamics increase the probability of recolonization and long-term persistence (Harrison & Quinn, 1989).

One caveat to our predictions is that we used a linear extrapolation to predict survival under future temperatures and flows, which should be validated or modified by an experimental study across the full range of conditions modeled. Nonetheless, we felt that this assumption was justified because two of the three lowest flows and some of the hottest temperatures on record occurred during our study period. Consequently, the extrapolation did not extend very far beyond observed conditions when considering the entire time series, especially for the composite scenario. A second caveat is that we assumed that only a single forcing factor affected parr-to-smolt survival, either temperature or flow, and not both. Certainly both factors could affect all populations. This would most likely occur under severe climate change and cause the populations to react similarly. The simplification we used should be robust under conditions more similar to today; in fact, it was the more moderate climate scenario that caused the most divergence between populations in our results. So, although the divergence may not last forever, it is still important in the trajectories of the populations. Furthermore, we present this analysis as a demonstration of potential effects, rather than an actual prediction. There is still quite a bit of uncertainty about the full relationship between environmental conditions and parr-to-smolt survival, and about the extent to which new behaviors or improved growth rates could help to reduce population-level effects.

Our approach of incorporating life-stage-specific climate effects into a life-cycle model is a powerful method for examining the impacts of these effects. Viability
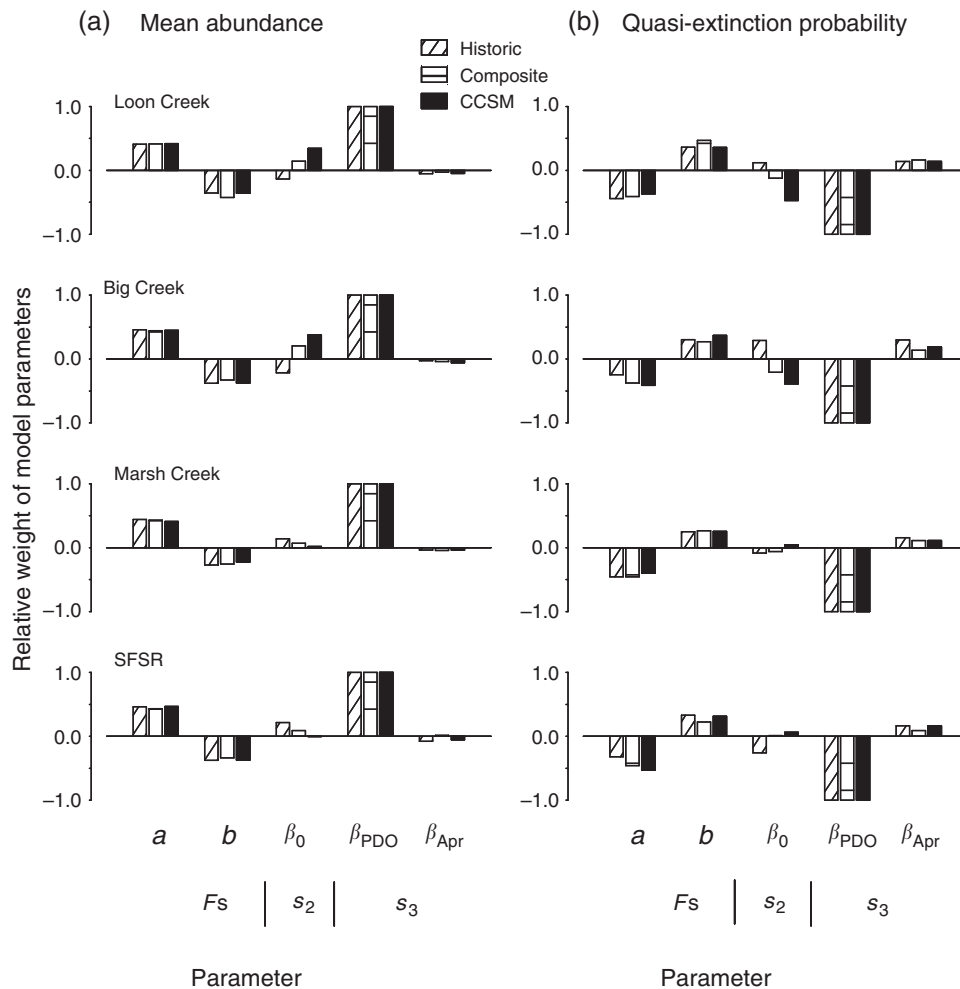
Fig. 7 This figure shows how sensitive model outcome, (a) mean abundance or (b) quasi-extinction probability is to changes in individual parameter values for each climate scenario: historic, the moderate composite scenario, or the hot/dry CCSM scenario. The relative weights for each parameter are the standardized multiple regression coefficients of model outcome as a function of all parameter values, where parameters vary within their respective 95% confidence intervals (see text). The most important parameter has a weight of ± 1. Each row shows the results for a different population. The parameters a and b are for the fertility equation, β_0 is the intercept of the freshwater survival equation, β_{PDO} and β_{Apr} are the intercept and coefficient for the April PDO index governing survival in the first year in the ocean. All of the remaining parameters were either directly correlated with shown parameters (see text) or had small effects and are not shown.

measures are the most important for managing at-risk populations, and it is not always obvious how changes in survival translate into changes in population viability. For example, moderate decreases in survival led to several-fold increases in the probability of falling below critical thresholds. Furthermore, the life-cycle approach allows for comparisons of effects across life stages and examinations of possible interactions. In our simulations, decreases in survival due to climate effects led to decreased population abundance, which led to increased fertility as a result of decreased densities. The importance of the density-dependent parameters (Fig. 7) indicates that these interactions are significant.

What do these results mean for the potential recovery of this threatened species? Most of the habitat in this basin is relatively pristine and protected in wilderness areas, so the primary challenge for recovery efforts will be to identify ways to mitigate threats posed by climate change. In some cases, it may be possible to increase flows and lower stream temperatures by decreasing water diversions and encouraging riparian cover in grazed areas. But improving conditions in other life stages will become even more important if juvenile survival continues to decline. Unfortunately, climate change will affect the entire life cycle of these fish. Although it is difficult to predict exactly how ocean

conditions will change, and especially how large-scale oscillations such as the PDO and El Niño will change, warm ocean periods in the past have been very unfavorable for Chinook salmon in the Pacific Northwest (Mantua *et al.*, 1997; Botsford & Lawrence, 2002), and extended periods of 'bad' ocean conditions can be catastrophic (Zabel *et al.*, 2006). In addition to effects on ocean survival, changing ocean conditions can affect age and size at maturity (Morita & Fukuwaka, 2007), which may influence fecundity. Furthermore, adult prespawn survival and fertility may decline due to high river temperatures (McCullough, 1999; King & Pankhurst, 2004; Battin *et al.*, 2007). Our results are, therefore, a conservative prediction of the effects of climate change. The stream-type Chinook salmon life history is characteristic of cooler water – they are typically found at higher latitudes and elevations than other life-history types (Healey, 1991). The entire migration and spawning strategy is adapted to a snow fall-dominated hydrological regime. Global warming will likely reduce potential habitat at lower elevations in the Pacific Northwest and at the southern edge of the range in California (Eaton & Scheller, 1996; Beechie *et al.*, 2006). This threat makes preserving existing populations at higher elevations, such as those studied here, a top conservation priority.

Acknowledgements

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Appendix A

Table A1 Metrics of population viability across 100 000 simulations of 88 years of population dynamics

Metric	Scenario	Loon Creek	Big Creek	Marsh Creek	SFSR
Parr-smolt survival					
	Current	0.217 (0.059)	0.128 (0.032)	0.212 (0.12)	0.142 (0.091)
	Composite	0.142 (0.043, −34%)	0.088 (0.023, −31%)	0.173 (0.092, −18%)	0.115 (0.064, −19%)
	CCSM	0.114 (0.036, −47%)	0.073 (0.019, −43%)	0.139 (0.061, −34%)	0.092 (0.04, −35%)
Mean abundance					
	Current	150.4 (18.1)	180.2 (21.4)	366.5 (59.2)	1181.4 (168.1)
	Composite	95.5 (13.2, −37%)	119.6 (15.2, −34%)	279.9 (48.9, −24%)	945.6 (140.2, −20%)
	CCSM	74.7 (11.3, −50%)	96.4 (12.8, −47%)	207.3 (40.4, −43%)	750.1 (115.4, −37%)
Minimum abundance					
	Current	11.9 (6.4)	16.1 (7.4)	26.5 (15.5)	88.8 (46.3)
	Composite	6.3 (3.8, −47%)	10.1 (4.9, −37%)	18.9 (11.8, −29%)	71.1 (37.6, −20%)
	CCSM	4.3 (2.9, −64%)	7.9 (4, −51%)	13.2 (8.9, −50%)	54.9 (30.2, −38%)
Quasi-extinction					
	Threshold	22	23	73	186
	Current	0.1405	0.0577	0.3595	0.182
	Composite	0.5722	0.2986	0.6213	0.3541
	CCSM	0.831	0.5414	0.8579	0.5876
Lambda					
	Current	0.984 (0.012)	0.993 (0.011)	0.999 (0.013)	0.998 (0.013)
	Composite	0.978 (0.012, −0.56%)	0.988 (0.011, −0.5%)	0.995 (0.012, −0.35%)	0.995 (0.012, −0.28%)
	CCSM	0.975 (0.013, −0.83%)	0.985 (0.012, −0.76%)	0.992 (0.013, −0.7%)	0.993 (0.012, −0.56%)

The standard deviation and percent change compared with the current climate are in parentheses.
SFSR, South Fork Salmon River.